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Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future?

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To examine the role of climatic extremes in structuring reef fish communities in the Arabian region, reef fish communities were visually surveyed at four sites within the southern Persian Gulf (also known as the Arabian Gulf and The Gulf), where sea-surface temperatures are extreme (range: 12–35° C annually), and these were compared with communities at four latitudinally similar sites in the biogeographically connected Gulf of Oman, where conditions are more moderate (range: 22–31° C annually). Although sites were relatively similar in the cover and composition of coral communities, substantial differences in the structure and composition of associated fish assemblages were apparent. Fish assemblages in the southern Persian Gulf held significantly lower estimates of abundance, richness and biomass, with significantly higher abundances of smaller sized individuals than Gulf of Oman assemblages. Functionally, southern Persian Gulf sites held significantly lower abundances of nearly all the common fish trophic guilds found on Gulf of Oman sites, although higher abundances of herbivorous grazers were apparent. These results suggest the potential for substantial changes in the structure of reef-associated fish communities, independent of changes in habitat within an environment of increasing fluctuations in oceanic climate. © 2010 The Authors

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Key words: Arabian Gulf; climate change; coral-reef fishes; Gulf of Oman; Persian Gulf; temperature.

INTRODUCTION

There is now a wealth of information showing that ecological communities will change substantially with increasing fluctuations in global climate, especially within tropical marine areas (Hoegh-Guldberg, 1999; Carpenter *et al.*, 2008; Gilman *et al.*,

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2008). Fluctuations in a range of physical variables, mediated by changes in global climate (e.g. sea-surface temperature and salinity) are predicted to affect directly the abundance, diversity, composition and demographic structure of the dominant habitat-forming corals in tropical marine communities, which will have indirect repercussions for associated fishes as a result of changes in habitat availability and quality (Purkis & Riegl, 2005; Baker *et al.*, 2008; Bradbury, 2008). There is increasing evidence, however, that fluctuations in physical variables associated with climate change may also have direct effects on a much wider array of tropical marine organisms than previously envisaged (Moore *et al.*, 2008; Przeslawski *et al.*, 2008), mediated through biochemical changes in their physiology, growth, reproduction and, ultimately, survival (Hurst, 2007; Chown & Gaston, 2008; Figueira *et al.*, 2009). Recent research indicates that changes in physical variables associated with climate change can have direct effects on individual fish physiology through reductions in growth, reproduction and survivorship (Munday *et al.*, 2008; Nilsson *et al.*, 2009), with the implication that these individual changes will result in larger changes to the wider fish communities in tropical systems (Munday *et al.*, 2008; Nilsson *et al.*, 2009; Wilson *et al.*, 2010). Given that fishes are considered among the most important fauna in tropical marine systems in terms of both economic and societal value to humans (Jackson *et al.*, 2001), understanding the implications of climate change on fish communities is of paramount importance.

In order to understand the potential effects of fluctuating physical extremes on fish communities in the future, it is appropriate to examine communities in areas already exposed to physical oceanic extremes. The north-eastern Arabian Peninsula is bounded by the Persian Gulf (also known as the Arabian Gulf and The Gulf) and the Gulf of Oman, with each distinguished by different oceanographic conditions (Sheppard *et al.*, 1992; Coles, 2003). The Persian Gulf is a shallow (mean depth <36 m), semi-enclosed basin connected to the Gulf of Oman and the wider Indian Ocean through the narrow Strait of Hormuz (Sheppard *et al.*, 1992). As a result of its shallow depth and restricted water exchange, the Persian Gulf is characterized by extreme sea-surface temperatures (SSTs) ranging from 12° C in winter to summer highs >36° C (Sheppard *et al.*, 1992; Sheppard, 1993; Riegl, 2001; Sheppard & Loughland, 2002). Hyper-saline conditions occur year-round with observations as high as 43 common (Reynolds, 1993), with moderate to low primary production found within the southern Persian Gulf [average of 1.0 mg m³ chlorophyll *a* levels using remote sensing data collected by SeaWiFS (September 1997 to May 2006) and MODIS-A (July 2002 to May 2006) satellite sensors] (Nezlin *et al.*, 2007). In comparison, the adjacent Gulf of Oman has deeper waters that are well mixed with those of the Indian Ocean, resulting in relatively mild seasonal changes in SSTs ranging from summer highs of 32° C to winter lows of 22° C (Coles, 1997; Bohm *et al.*, 1999; Schils & Wilson, 2006). Fluctuations in salinity are relatively mild (35–37), while substantial upwelling along the coastal margin leads to a relatively high mixed layer primary production of 900 mgC m⁻² day⁻¹ (Brock *et al.*, 1994; Nezlin *et al.*, 2007). These two systems make for an interesting and appropriate comparison for the effects of changing climate on oceanic processes, as they are biologically and geographically connected with one another, but experience such different environmental conditions. Additionally, given that the Persian Gulf reefs persist despite experiencing the highest variability in annual temperature encountered by any coral reefs (Kinsman, 1964; Sheppard *et al.*, 2000), they may serve as

a useful proxy for the implications of changing ocean temperatures on a global scale (Riegl, 2003).

Despite environmentally different regimes between the two regions (Coles, 1997, 2003), there are broad similarities in benthic community structure between the Persian Gulf and Gulf of Oman. The Persian Gulf forms a biogeographic subset of the Indian Ocean, with close faunal affinity with communities in the Gulf of Oman (Sheppard, 1987; Sheppard & Sheppard, 1991). In addition, coral reef communities found within the southern areas of the Persian Gulf (mainly encapsulating the United Arab Emirates), although showing lower diversity are highly similar topographically to those found at similar latitudes within the Gulf of Oman. Within both regions stony coral cover is limited to areas of hard substratum, which can result in relatively patchy coral distribution (Wilson, 2007; Burt *et al.*, 2008). Within areas suitable for coral growth, substantial coral reef communities will develop in both regions, and can be dominated by a range of branching, columnar, encrusting, laminar and massive morphologies (Sheppard *et al.*, 1992; Coles, 2003).

This research examined the structure of coral reef communities throughout the north-eastern Arabian Peninsula, encapsulating areas both within the southern Persian Gulf and at similar latitudes within the Gulf of Oman. In particular, the structure and composition of reef-associated fish communities was compared between regions. To avoid the confounding factors of benthos *v.* environmental factors, this study focused on comparing fish communities within areas of similar coral structure. It was hypothesized that within areas of similar coral reef structure substantial differences in the structure and composition of fish communities would be apparent. In line with previous assessments of biodiversity estimates between the Persian Gulf and Gulf of Oman, it was predicted that fish communities within the southern Persian Gulf were more likely to show reduced diversity than Gulf of Oman communities, due to the relatively recent geological origin of the Persian Basin as well as the background physiological stress associated with extremes in physical variables (Price, 2002; Coles, 2003; Schils & Wilson, 2006). It was also predicted, however, that physiological stress associated with the physical extremes of the Persian Gulf may also have substantial negative effects on species growth (Hurst, 2007), with concomitant negative effects on community biomass and size structure. It was also predicted that there would be little difference in the guild structure of communities between regions, with the majority of differences associated with site-specific differences in available food and habitat.

MATERIALS AND METHODS

Between October and November 2008, the structure and composition of coral reef communities was examined between the southern Persian Gulf (Ras Ghanada, Sadiyaat, Ras Hasyan and Saih Al-Shaib) and Gulf of Oman (Dibba, Al-Aqah, Al-Ghattan and Al-Jazira) (Fig. 1). Each site was similar in terms of depth (*c.* 5–6 m), distance to shore (*c.* 100 m) and latitude (Fig. 1). Logistic difficulties precluded multiple surveys of coral reef communities in both regions throughout the year. In addition, substantial reductions in the abundance of Persian Gulf fish communities, due to seasonal migrations of fish communities off reefs, occur in the winter months (Coles & Tarr, 1990; Burt *et al.*, 2009). Therefore, to reduce any seasonal bias in fish community abundance between regions, all surveys were conducted during the northern hemisphere's summer months.

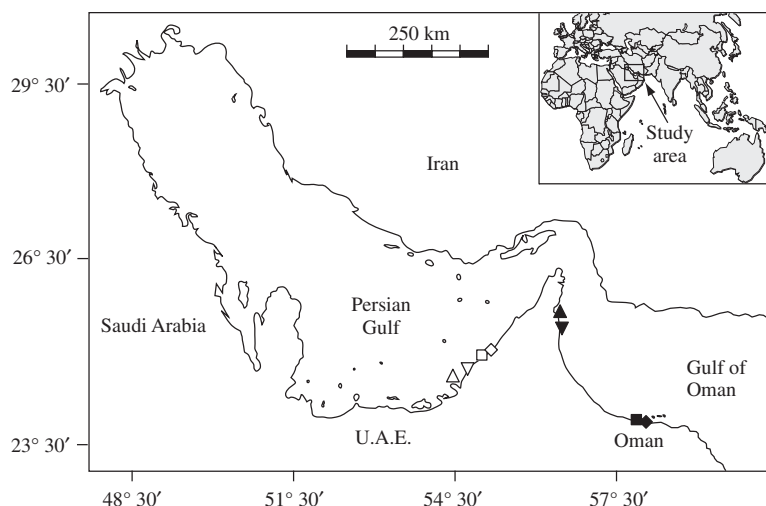


FIG. 1. Sampling sites in the Persian Gulf (Δ , Ras Ghanada; ∇ , Sadiyaat; \square , Ras Hasyan; \diamond , Saih Al-Shaib) and Gulf of Oman (\blacktriangle , Dibba; \blacktriangledown , Al-Aqah; \blacksquare , Al-Ghattan; \blacklozenge , Al-Jazira).

Fishes were counted visually by scuba along eight 5 m \times 30 m belt transects. All fishes were identified to species (Randall, 1995) and categorized into 50 mm interval size classes (total length, L_T) for later conversion to biomass based on species-specific growth coefficients (Froese & Pauly, 2009). Fish species were also classified by primary feeding guild (*i.e.* corallivore, grazer, invertivore, piscivore, piscivore–invertivore, planktivores and scraper and excavator) (Randall, 1995; Froese & Pauly, 2009). Coral communities were sampled using 0.25 m² quadrats photographed at 3 m intervals on the same transects sampled for fishes (11 quadrats per transect) (Burt *et al.*, 2009). Photographs were analysed using 50 random point intercepts in coral point count with Excel extensions (CPCe) software (Kohler & Gill, 2006), with all corals identified to species and classified by dominant morphology (Veron, 2000). Coral morphological categories were branching, columnar, encrusting, laminar and massive.

Prior to multivariate analysis, all fishes and coral species occurring in <5% of samples were removed in order to reduce the influence of outliers (Tabachnick & Fidell, 2001; McCune & Grace, 2002). To examine whether there were significant differences in coral cover between regions and among sites within regions, data were square-root transformed and compared using nested ANOVA. To compare the structure of fish communities between regions and among sites within regions, data were $\log_{10}(n + 1)$ transformed and the abundance and biomass compared using nested ANOVA, with *post hoc* Tukey's tests used to identify significantly different groups. As estimates of abundance and richness in a sample are correlated (Gotelli & Colwell, 2001), rarefaction techniques were utilized [using the EcoSim programme of Gotelli & Entsminger (2009)] to rarefy and compare fish species richness between regions (southern Persian Gulf and Gulf of Oman). Rather than arbitrarily using a single number of individuals, species richness was rarefied at 1000, 2000, 3000, 4000 and 5000 individuals. The programme randomly chooses 1000 individuals, for example, and then determines species richness. The procedure is repeated 1000 times to find the average expected species richness ($\pm 95\%$ C.I.). Fish size-class distributions were also compared between regions using χ^2 tests on the proportional abundance of fishes in each L_T class, based on the mean abundance of fishes in transects at each site, averaged across sites in each region.

Differences in multivariate fish community structure between the southern Persian Gulf and the Gulf of Oman, both in terms of species and guild composition, were compared graphically using ordination scatterplots from non-metric multidimensional scaling (NMS), with significance of differences tested using analyses of similarity (ANOSIM) (Clarke & Warwick, 2001). ANOSIM produces a test statistic, R , which assesses the null hypothesis that there are no differences among groups; an R -value > 0.5 indicates strong differences among groups (Clarke

& Warwick, 2001). Fish species and guilds driving differences among groups were then identified using similarity percentage analysis (SIMPER), which quantifies the contribution of each species or guild to dissimilarity between groups (Clarke & Warwick, 2001).

A linear regression was used to determine whether fish species richness, abundance or biomass was associated with the amount of coral cover. In addition, correlations in the multivariate structure of fish and coral communities were tested with RELATE (Clarke & Warwick, 1994), using both fish species and guild structure *v.* coral species and morphology structure. RELATE is a non-parametric comparative (Mantel-type) test which tests the hypothesis of no relation between two multivariate groups, and produces a Spearman's rank correlation statistic (ρ) and a *P*-value based on a comparison with a randomized set of samples.

RESULTS

Nested ANOVAs showed significantly lower fish species abundance and biomass in the southern Persian Gulf compared with the Gulf of Oman (ANOVA, $F_{1,56} = 22.3$ and 43.1 , respectively, $P < 0.01$ each) and significant variation among sites within regions (ANOVA, $F_{6,56} = 5.6$, 12.7 and 13.8 , respectively, $P < 0.001$ each) (Table I). Rarefaction showed that Gulf of Oman communities held substantially higher species richness, when comparing the same number of individuals, to southern Persian Gulf communities. When sampling 4000 individuals in the southern Persian Gulf (the maximum number of individuals found for this region was 4134), the expected richness was 28.9 species (± 0.1 95% C.I.). Sampling the same number of individuals in the Gulf of Oman, species richness was 61.6 species (± 4.0 95% C.I.).

Ordination indicated substantial differences in the structure of fish communities between the southern Persian Gulf and the Gulf of Oman both in terms of species and guild composition (Fig. 2), and these differences were shown to be strong and significant in ANOSIM (species composition: $R = 0.78$, $P < 0.001$; guild composition: $R = 0.74$, $P < 0.001$). SIMPER indicated 82.1% dissimilarity in species composition between regions; species driving these differences are indicated in Table II. Of the 28 species that contributed to community dissimilarity, over half were more abundant in the Gulf of Oman than the southern Persian Gulf (Table II).

TABLE I. Mean \pm S.E. species richness and abundance at each site within the Persian Gulf and Gulf of Oman. Different superscript lower case letters indicate significant differences between sites within each region based on Tukey's tests

	Richness (150 m ⁻²)	Abundance (150 m ⁻²)	Biomass (kg ha ⁻¹)
Southern Persian Gulf			
Ras Ghanada	11.1 \pm 0.7 ^a	140.4 \pm 18.7 ^{a,b}	86.3 \pm 19.6
Sadiyaat	11.9 \pm 0.7 ^a	309.1 \pm 76.6 ^b	394.8 \pm 105.1
Ras Hasyan	6.5 \pm 0.5 ^b	22.9 \pm 2.3 ^c	9.4 \pm 2.3
Saih Al-Shaib	8.3 \pm 1.1 ^{a,b}	63.3 \pm 17.2 ^{a,c}	68.9 \pm 19.2
Gulf of Oman			
Dibba	18.3 \pm 2.8 ^a	329.3 \pm 54.3 ^a	883.2 \pm 120.5 ^a
Al-Aqah	10.0 \pm 1.0 ^b	99.8 \pm 29 ^b	140.8 \pm 42.6 ^b
Al-Ghattan	14.0 \pm 0.7 ^{a,b}	171.8 \pm 24.5 ^{a,b}	504.9 \pm 174.6 ^{a,b}
Al-Jazira	13.4 \pm 2.2 ^{a,b}	115.9 \pm 31.1 ^b	320.3 \pm 123.9 ^b

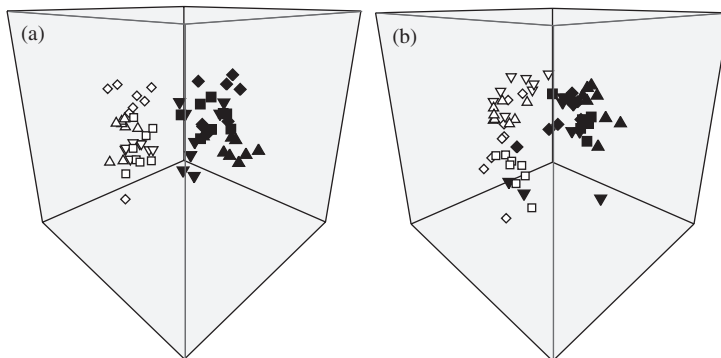


FIG. 2. Ordination scatterplot of fish communities based on (a) species structure and (b) guild structure in transects at each of four sites in the southern Persian Gulf (Δ , Ras Ghanada; ∇ , Sadiyaat; \square , Ras Hasyan; \diamond , Saih Al-Shaib; stress = 0.14) and the Gulf of Oman (\blacktriangle , Dibba; \blacktriangledown , Al-Aqah; \blacksquare , Al-Ghattan; \blacklozenge , Al-Jazira; stress = 0.09).

The size structure of fish communities differed significantly between the southern Persian Gulf and the Gulf of Oman (Fig. 3; $\chi^2 = 85.8$, d.f. = 7, $P < 0.001$). There was relatively higher abundance of fishes in the 50–100 mm L_T class in the Persian Gulf, with abundance in all other L_T classes higher in the Gulf of Oman. There were virtually no fishes (0.3%) >200 mm L_T in the southern Persian Gulf, while there was an order of magnitude more fishes in >200 mm L_T classes in the Gulf of Oman, with fish abundance showing a near exponential decline with each successive size-class here compared with the truncated distribution in the southern Persian Gulf (Fig. 3).

In terms of feeding guilds, there was 78.8% dissimilarity in guild structure between regions, with nearly half of this dissimilarity resulting from differences in the abundance of planktivores and grazers between regions (Table III). Nested ANOVAs indicated that only grazers were more abundant in the southern Persian Gulf ($F_{1,56} = 193.9$, $P < 0.001$), while there were significantly more planktivores, piscivores,

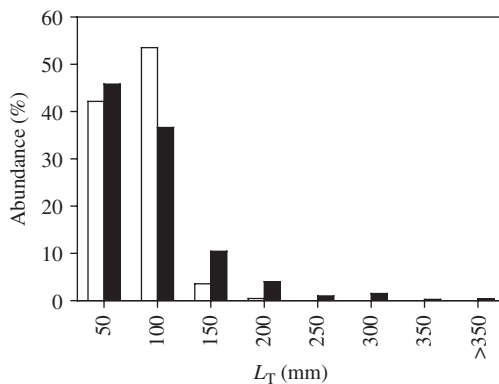


FIG. 3. Relative abundance of fish in each total length (L_T) class in the southern Persian Gulf (\square) and the Gulf of Oman (\blacksquare).

TABLE II. Species differences in fish community structure between the southern Persian Gulf and the Gulf of Oman. Mean abundance in each region and individual and cumulative contribution (δ %) to dissimilarity from SIMPER are indicated

Species	Common name	Functional guild	Southern Persian Gulf			Cumulative δ (%)
			mean number per 150 m ²	mean number per 150 m ²	Contribution δ (%)	
<i>Pomacentrus leptus</i>	Slender damsel	Planktivore	0.3	26.8	6.3	6.3
<i>Pomacentrus aquilus</i>	Dark damsel	Grazer	18.4	0.0	6.3	12.6
<i>Lutjanus ehrenbergii</i>	Blackspot snapper	Piscivore and invertivore	39.3	9.5	6.1	18.6
<i>Cephalopholis hemistiktos</i>	Yellowfin hind	Piscivore	0.3	10.0	5.2	23.9
<i>Pomacanthus maculosus</i>	Yellowbar angelfish	Invertivore	6.2	0.5	5.2	29.1
<i>Scolopsis ghanam</i>	Arabian monocle bream	Invertivore	14.7	17.8	4.9	34.0
<i>Dascyllus trimaculatus</i>	Threespot dascyllus	Planktivore	0.0	7.7	4.7	38.6
<i>Chromis xanthopterygia</i>	Yellowfin chromis	Planktivore	0.0	21.2	4.6	43.3
<i>Lutjanus fulviflamma</i>	Dory snapper	Invertivore	8.1	0.4	4.5	47.8
<i>Parupeneus margaritatus</i>	Pearly goatfish	Invertivore	10.8	4.8	4.4	52.2
<i>Pomacentrus trilineatus</i>	Threeline damsel	Grazer	20.4	0.0	3.6	55.8
<i>Caesio varilineata</i>	Variable-lined fusilier	Planktivore	0.0	20.4	3.6	59.3
<i>Abudefduf vaigiensis</i>	Indo-Pacific sergeant	Planktivore	0.0	13.5	3.5	62.8
<i>Chaetodon nigropunctatus</i>	Blackspotted butterflyfish	Corallivore	1.9	4.7	3.5	66.3
<i>Plectorhinchus sordidus</i>	Sordid rubberlip	Piscivore and invertivore	4.0	0.6	2.5	68.8
<i>Ostracion cyanurus</i>	Bluetail trunkfish	Invertivore	0.0	3.1	2.3	71.1
<i>Pseudochromis persicus</i>	Bluespotted dottyback	Invertivore	2.0	0.0	2.3	73.4
<i>Thalassoma lunare</i>	Moon wrasse	Invertivore	0.0	4.0	2.2	75.6
<i>Carangoides bajad</i>	Orangespotted trevally	Invertivore	1.0	2.2	2.2	77.7
<i>Scarus persicus</i>	Gulf parrotfish	Scrapers and excavators	0.1	2.8	2.1	79.8

TABLE II. Continued

Species	Common name	Functional guild	Southern Persian Gulf (mean number per 150 m ²)	Gulf of Oman (mean number per 150 m ²)	Contribution δ (%)	Cumulative δ (%)
<i>Acanthopagrus bifasciatus</i>	Two-bar seabream	Piscivore and invertivore	1.5	0.3	1.9	81.7
<i>Lethrinus nebulosus</i>	Spangled emperor	Piscivore and invertivore	0.6	2.6	1.7	83.5
<i>Epinephelus stoliczkae</i>	Epaulet grouper	Piscivore and invertivore	0.0	0.8	1.3	84.8
<i>Zebrasoma xanthurum</i>	Yellowtail tang	Grazer	0.0	0.8	1.2	86.0
<i>Pseudochromis alabracensis</i>	Orange dottyback	Invertivore	0.8	0.1	1.2	87.2
<i>Labroides dimidiatus</i>	Bluestreak cleaner wrasse	Invertivore	0.0	2.2	1.1	88.3
<i>Halichoeres marginatus</i>	Dusky wrasse	Invertivore	0.0	6.4	1.1	89.3
<i>Plectorhinchus gaterinus</i>	Blackspotted rubberlip	Piscivore and invertivore	1.9	0.0	1.0	90.4

TABLE III. Guild differences in fish community structure between the southern Persian Gulf and the Gulf of Oman. Mean abundance per 150 m² in each region and individual and cumulative contribution (δ %) to dissimilarity from SIMPER are indicated

Guilds	Southern Persian Gulf	Gulf of Oman	Contribution (δ %)	Cumulative (δ %)
Planktivores	0.3	92.1	28.7	28.7
Grazers	39.0	1.7	18.9	47.6
Piscivores and invertivores	48.1	19.7	13.3	60.9
Piscivores	0.3	10.0	12.7	73.6
Invertivores	44.2	46.7	10.5	84.0
Corallivores	1.9	5.6	9.0	93.0
Scrapers and excavators	0.2	3.4	7.0	100.0

corallivores and scraper and excavators in the Gulf of Oman ($F_{1,56} = 163.9, 141.1, 18.9,$ and $33.7,$ respectively, $P < 0.001$ each); the abundance of invertivores and piscivore–invertivores did not differ significantly between regions ($F_{1,56} = 0.6$ and $3.2,$ respectively, $P > 0.05$ each) (Fig. 4).

Coral cover was comparable between the southern Persian Gulf and the Gulf of Oman ($F_{1,56} = 3.6, P > 0.05$), but showed variation among sites within regions ($F_{6,56} = 8.1, P < 0.001$; Fig. 5). Regression analyses showed that there was a significant relationship between fish abundance and total coral cover in transects across regions ($r^2 = 0.08, \text{d.f.} = 62, P < 0.05$), but there was no relationship between coral cover and fish biomass or fish species richness ($r^2 = 0.02$ and $0.01,$ respectively, $\text{d.f.} = 62, P > 0.05$ each). In terms of overall community structure, fish and coral communities were shown to be only weakly correlated with each other in RELATE in terms of both fish species and guild structure *v.* coral species and growth form structure (Table IV).

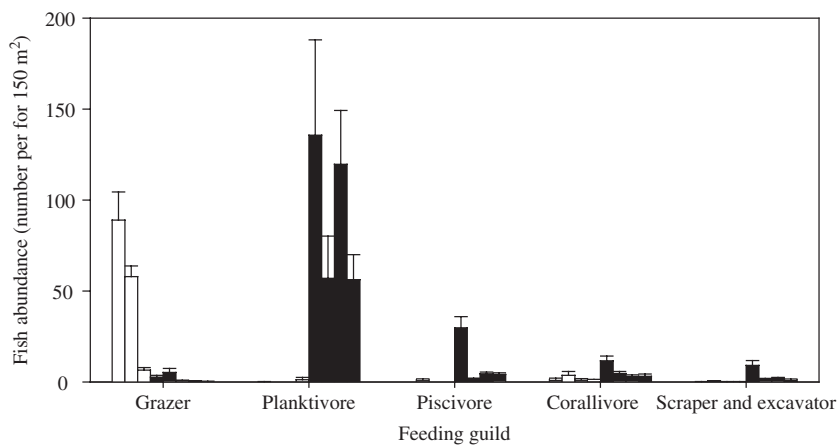


FIG. 4. Mean \pm S.E. abundance of fishes in feeding guilds at sites within the southern Persian Gulf (□) *v.* the Gulf of Oman (■). Sites, in order of appearance (left to right), are Ras Ghanada, Sadiyaat, Ras Hasyan and Saih Al-Shaib (southern Persian Gulf), and Dibba, Al-Aqah, Al-Ghattan and Al-Jazira (Gulf of Oman).

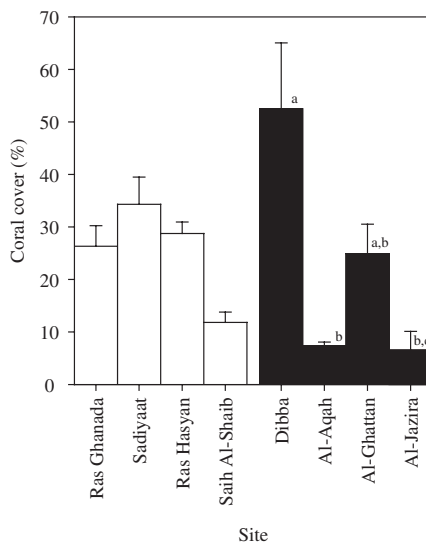


FIG. 5. Mean \pm S.E. coral cover at each site in the southern Persian Gulf (\square) and the Gulf of Oman (\blacksquare). Different lower case letters indicate significant differences ($P < 0.05$) between sites in the Gulf of Oman based on Tukey's tests; there were no differences ($P > 0.05$) among sites in the southern Persian Gulf.

DISCUSSION

The southern Persian Gulf is characterized by extreme environmental conditions, with physical extremes not observed in tropical reefs anywhere else in the world (Sheppard *et al.*, 1992; Coles, 2003; Riegl, 2003). Despite these conditions, diverse and abundant coral and coral-associated fish communities do develop in this area (Riegl, 1999; Burt *et al.*, 2008), indicating that a variety of reef fauna can survive at or above the elevated sea temperatures predicted for much of the world in the coming decades (IPCC, 2007). This observation, however, is not without a note of caution: the results of the work here, and earlier work on benthic communities in the region (Sheppard, 1987; Sheppard & Sheppard, 1991; Coles, 2003), show that while a number of species can tolerate these extreme conditions, the communities are generally lower in diversity and abundance, and function differently, than those in more benign environments (Sheppard *et al.*, 1992; Coles, 2003).

Although there was a significant relationship between fish abundance and total coral cover, the majority of fish assemblage parameters (*i.e.* biomass, richness and guild structure) had little relationship to coral cover, coral species structure or growth

TABLE IV. Spearman's rank correlation (ρ) between multivariate fish communities, in terms of species and guild structure, and coral communities, in terms of species and growth forms, based on RELATE analyses ($P < 0.001$)

	Fish species structure	Fish guild structure
Coral species structure	0.45	0.34
Coral growth forms	0.36	0.29

forms throughout regions. Such low concordance between demographic variables and coral assemblage structure shows that assemblages within both regions may be less tightly associated with the live coral structure than the reef structure itself (Graham *et al.*, 2006). Indeed, there is still little agreement between researchers on the importance of live coral *v.* reef complexity in structuring reef fish communities (Graham *et al.*, 2006; Feary *et al.*, 2007; Pratchett *et al.*, 2008). Particularly within the southern Persian Gulf, but also within the Gulf of Oman, substantial seasonal changes in coral cover can occur, mainly through overgrowth of turfing and fleshy macroalgae in spring months (Riegl, 1999; Burt *et al.*, 2008), but also through warm-water bleaching (Riegl, 1999) and harmful algal bloom development (Richlen *et al.*, 2010). Such seasonal variations in live coral cover may have resulted in fish assemblages becoming adapted to non-coral-dominated communities, where both habitat availability and feeding resources are more associated with seasonal changes in available benthic resources than with a stable coral reef platform (Riegl, 1999).

Despite little association between coral and fish community structure, there were broad differences in the abundance and biomass of fish communities between regions, which may be associated with either temperature or salinity effects (*i.e.* osmotic stress) on fish physiology (Hurst, 2007). Temperature and salinity are the primary variables regulating aquatic species bioenergetics (Kitchell *et al.*, 1977), and fluctuations in ambient levels of either variable can substantially affect the rate and efficiency of physiological processes such as feeding, respiration, faecal egestion rates and ultimately growth (Kitchell *et al.*, 1977; Hurst, 2007). Even under natural conditions, fishes will experience a range of temperature and salinity both spatially and temporally due to behavioural activities, and such variations may have substantial effects on the physiology of animals (Hurst, 2007). Within the southern Persian Gulf, with rapid temporal fluctuations between maximum and minimum temperature between seasons and amid relatively high background salinity levels (which fluctuate with season), the physiological optima for fishes may exist for limited periods during the year (*i.e.* between summer and winter). Therefore, key bioenergetic variables controlling physiological mechanisms may only be maximized for a short time frame during their annual cycle (Hurst, 2007; Figueira *et al.*, 2009), and have a substantial effect on the development and structure of fish communities. Under predictions of increasing fluctuations in global oceanic temperature and salinities (IPCC, 2007), the structure of tropical reef fish communities may then undergo increasing periods of physiological stress (Munday *et al.*, 2008; Nilsson *et al.*, 2009) which may affect the demographic mechanisms important in structuring assemblages, and have flow-on effects to the abundance and biomass of communities (Munday *et al.*, 2008).

High average sea-surface temperatures can have a substantial effect on plankton community composition; communities can become less productive within higher temperatures as longer, less-productive planktonic food chains are favoured (McKinnon *et al.*, 2007). In this respect, levels of primary productivity differ between regions, with much higher productivity in the Gulf of Oman than Persian Gulf, due to upwelling of cold and nutrient-rich waters along the Omani coastline associated with the summer monsoonal conditions within the Arabian Sea (Schils & Wilson, 2006). In contrast, minor upwelling events combined with little riverine input have resulted in the Persian Gulf being a relatively nutrient-poor environment (Sheppard *et al.*, 1992; Nezlin *et al.*, 2007). Such divergence in primary productivity, associated with differences in physical variables controlling productivity between regions (Sarmiento *et al.*,

2004; Brown *et al.*, 2010), may underpin differences in the abundance and diversity of fish communities between regions (Brown *et al.*, 2010). There is now increasing evidence that warming of oceanic waters can have a substantial effect on the distribution and abundance of ocean primary production (Richardson & Schoeman, 2004; Behrenfeld *et al.*, 2006) and these changes have been linked to changes in higher trophic level organisms (Richardson & Schoeman, 2004; Beaugrand *et al.*, 2008). Within the Persian Gulf, the physical extremes (*i.e.* high maximum summer temperatures) may have a substantial negative effect on the primary productivity within the Persian Gulf, which may then have flow-on effects to the abundance and diversity of fishes within this region (Richardson & Schoeman, 2004; Beaugrand *et al.*, 2008).

There were broad differences in the size structure of assemblages between regions, indicative of a low average body size of fish assemblages within the southern Persian Gulf. Although both regions were dominated by relatively small-bodied fishes, the Gulf of Oman held significantly higher abundances of fishes >200 mm L_T . Although there is little information on fishing at the sampling sites in either region, anecdotal evidence suggests that all sites surveyed are exposed to relatively low or moderate fishing activity. Therefore, the lower abundance of large-sized fishes in the Gulf of Oman was not likely to be due to fishing effects. Such differences in assemblage size structure may then be influenced by a complex interaction between both environmental and demographic factors (Fonseca & Cabral, 2007; Feary *et al.*, 2009). In general, however, individuals tend to reach smaller maximum sizes and have shorter lives in physically stressful environments (Hurst, 2007; Munday *et al.*, 2008), and recent evidence suggests that species within such environments may show reduced growth rates (Figueira *et al.*, 2009). Reductions in species growth rate may have substantial effects on the demographic processes structuring their populations. In particular, there will be an increase in time to sexual maturity (Booth, 1995), reducing lifetime gamete production and potentially both local and regional replenishment. In addition, reductions in growth rate may also indirectly affect species mortality, increasing the length individuals remain in small, predator-vulnerable sizes thereby enhancing their potential for predation risk (Holbrook & Schmitt, 2002). While such theoretical changes in fish communities within physically stressful environments are yet to be rigorously tested (Munday *et al.*, 2008; Wilson *et al.*, 2010), communities utilizing such environments (such as within the southern Persian Gulf) provide a unique opportunity to examine such predictions and will be important in understanding the potential repercussions of climate change on the ecological structure of marine communities.

This study has shown that the southern Persian Gulf has much lower fish species richness than the adjacent Gulf of Oman. This finding is in corroboration with similar studies arguing that this fauna represents a biogeographic subset of those in the Indian Ocean that have re-colonized the area following flooding after the last glacial period (Sheppard & Sheppard, 1991; Coles, 2003). Such low richness, however, is likely also due to the physical extremes within the Persian Gulf (*e.g.* variation in temperature and salinity) for which few Indian Ocean species have been able to adapt and tolerate (Coles & Tarr, 1990; Randall, 1995). In corroboration, even within the Persian Gulf patterns in species richness are associated with changes in physical extremes. For example, within the deeper waters of the northern part of the Persian Gulf (along the Iranian coastline), where variations in temperature and salinity are less extreme, communities are noted as being richer in species than waters in the southern region (Price *et al.*, 1993). In parallel, in the south-western basin, highest

species richness has been observed near the deep-water offshore islands of Saudi Arabia, with diversity declining north and east of this area, probably as a result of more extreme water salinity (Price *et al.*, 1993).

Guild structure changed considerably from the southern Persian Gulf to the Gulf of Oman. This was predominantly due to lower abundances of most trophic guilds within the southern Persian Gulf compared with the Gulf of Oman, and a higher abundance of herbivorous grazers. It can be predicted that differences in guild structure may be associated with seasonal changes in benthic habitat, with the southern Persian Gulf holding relatively high cover of seasonally occurring turfing and fleshy macroalgae (Riegl, 1999; Burt *et al.*, 2008). In this respect, the much higher numerical abundance of corallivores within the Gulf of Oman will be due to more widespread coral cover throughout this coastline (Sheppard *et al.*, 1992; Coles, 1997, 2003). Reduced abundances of piscivores in the southern Persian Gulf are more likely to be due to reductions in the average abundance of fish assemblages within this region, as piscivore abundance will usually mirror prey abundance (Stewart & Jones, 2001). Substantial differences in the abundance of planktivores between regions were also found, with substantially smaller abundances within the southern Persian Gulf. As the majority of planktivores within the eastern Arabian Peninsula are smaller bodied fishes (*i.e.* Pomacentridae and Caesionidae), it can be predicted that this trophic group may be more negatively affected by extremes in environmental conditions within the southern Persian Gulf (*i.e.* high temperature variations) than larger species, due to the metabolic demands of smaller size fishes (Munday & Jones, 1998).

Understanding whether the patterns reported in this work are applicable to reefs globally will be important in determining the wider implications of this research. Between the Gulf of Aden and southern Red Sea regions, similarities in the change in physical variables to that found between the southern Persian Gulf and Gulf of Oman are present (Roberts *et al.*, 1992). Both temperature and salinity show an increasing gradient moving from the Gulf of Aden to the Red Sea, with average summer temperatures of 28 and 30° C and summer salinities of 36.5 and 42.0, respectively (Roberts *et al.*, 1992; Sheppard *et al.*, 1992). There is also a change in productivity between regions, with inflowing waters from the Gulf of Aden being richer in nutrients than the oligotrophic waters of the Red Sea, with an abrupt drop in nutrient concentration north of 19° N (Roberts *et al.*, 1992). Such changes in physical variables have resulted in a zoogeographic boundary for species distribution, with substantial reductions in the abundance and diversity of reef fish communities when comparing the Gulf of Aden and the Red Sea (Roberts *et al.*, 1992; Kemp, 1998). Although low levels of available coral reef habitat in the southern Red Sea may have a substantial effect on reef fish abundance and diversity (Roberts *et al.*, 1992; Kemp, 1998), such differences in reef fish community structure may also be associated with the substantial changes in physical variables between regions (Roberts *et al.*, 1992).

There were substantial differences in the structure and composition of reef fish communities in the southern Persian Gulf and the Gulf of Oman, despite these being biogeographically connected, indicating the importance of environmental extremes in structuring fish assemblages. Although the possible role of high water temperature in determining community composition and abundance has been emphasized, extremes in salinity levels, along with relatively low primary productivity will also act synergistically to have substantial effects on the structure and assembly of southern Persian Gulf communities. Although there is still little research investigating the

role of fluctuations in ocean processes in structuring reef-associated fish communities (Roessig *et al.*, 2004; Harley *et al.*, 2006; Munday *et al.*, 2008), the results of this work suggest that measurable differences in major oceanographic variables dominating regions may have substantial flow-on effects to the composition and structure of the associated reef fish community.

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